

APPENDIX A

CONDITIONS FOR BLOOM DEVELOPMENT: INTERPLAY AMONG BIOGEOCHEMICAL, BIOLOGICAL, AND PHYSICAL PROCESSES

Overview

In temperate estuaries, the spring bloom typically is dominated by diatoms and occurs when freshwater delivers adequate amounts of N, P, and Si and other nutrients to the system. In deep estuaries, the spring freshwater inflow also provides for vertical density stratification where enough of the euphotic zone resides near the surface to allow phytoplankton to achieve net biomass production (i.e., total photosynthesis minus respiration is positive). During this time solar insolation and water temperature are on the increase. For a bloom to develop, other conditions must be met. Physical flushing and local dispersion of a water parcel must be less than the doubling time for cells. Biological grazing rate must not be so large as to consume phytoplankton faster than cells' doubling time.

Biogeochemical Processes

Three aspects of N and P biogeochemistry help explain whether N or P dominates nutrient limitation in estuaries (i.e., relative nitrogen fixation rates, denitrification, and sediment regeneration of P). The first aspect involves evidence suggesting that nitrogen fixation is less effective in marine than in freshwater systems in making up nitrogen deficits (Howarth 1988; Schindler 1974). This finding has major implications for long-term coastal and open-ocean nutrient overenrichment, because N fixation is so inefficient that any balance in the N versus P limitation occurs in terms of geological time.

The second aspect involves one of the greatest differences in nutrient biogeochemical cycles between freshwater and marine systems. The superior capacity of freshwater versus marine systems to retain P in sediments through interactions with iron has profound implications. Nearly all the P deposited in marine sediments is remineralized annually (Caraco et al. 1990) and depends heavily on the sulfate concentration, which can be used as a surrogate for salinity. Thus, P in freshwater sediments is bound more tightly, and proportionally less is released back into the water column. Also, P release from marine sediments is temperature dependent, and its maximum release during the summer helps explain the tendency for increasing water column concentrations of P to occur during that season in many estuaries (Nixon et al. 1980). Estuaries with a well-developed tidal freshwater zone might be expected to be more P-limited than estuarine systems with small tidal fresh areas.

More details on nutrient cycling in subtropical and tropical marine waters, systems much less studied than northern temperate estuaries, are provided by Bianchi et al. (1999). The extensive coastal wetland systems (e.g., marshes and mangroves) that border the Gulf of Mexico provide environments where chemical transformations and storage of nutrients occur. Also, extensive seagrass meadows apparently tie up inorganic N and P so that relatively less remains free in the water column. In general, DIN and PO₄ concentrations are much lower in northern Gulf river-dominated estuaries (e.g., Mobile and Apalachicola Bays) than similar U.S. East Coast systems, presumably because of the lower point sources. Local groundwater sources are important and water quality managers should be aware of them. However, local estuarine point sources of N and P may alter nonpoint source patterns (e.g., paper mills and wastewater treatment facilities) (Livingston 2001a).

Denitrification is the third aspect that plays a role in N limitation in estuaries and coastal waters (Nixon et al. 1996). Denitrification is the process whereby nitrate is converted to gaseous N₂ and N₂O and thereby made unavailable. Denitrification provides a sink for N in estuarine systems. Shelf waters generally are too deep to provide enough sediment-water column contact for a quantitatively significant magnitude of denitrification to occur. Bottom-water anoxia limits nitrification and hence denitrification

in the high-sulfide sediments where nitrification and denitrification are coupled (Jenkins and Kemp 1984). Knowledge of the magnitude of denitrification can help the water quality manager predict the nutrient overenrichment response of an estuary, because N that is denitrified is largely unavailable to support primary production.

Biological Processes

The relative importance of biological grazing should be assessed, because when a nutrient problem occurs it is evidence that enrichment has exceeded the ability of the system to maintain a steady state in net biomass production at pre-enrichment levels. For example, major changes in the biology of estuaries in terms of particle filtering capacity (e.g., oysters: Newell 1988) and probably filter feeding finfish (e.g., menhaden) can modify phytoplankton primary production, although the quantitative effectiveness of such cropping is scientifically unsettled. Nutrient overenrichment may drive marine waters toward smaller algae and other microbes (Jonas 1992) where organic carbon flows more to the microbial loop (Hassett et al. 1997), versus more direct flow to copepods and higher trophic levels (e.g., finfish). This shift in the food web may be a significant factor in how estuaries “assimilate” increased nutrient inputs (Roelke et al. 1999; Roelke 2000).

Physical Processes and Factors

Conceptual Framework

Smith (1984) argued that there is no inherent difference in nutrient limitation between lakes and the ocean. Abundant evidence indicates that phytoplankton net primary production in north temperate lakes tends to be P limited, and phytoplankton production in the ocean as a whole is potentially moderately P limited but at higher P concentrations than lakes. This conclusion is supported by the observation that TN:TP ratios of the surface ocean are usually well in excess of the Redfield ratio (Guildford and Hecky 2000). Local deviations have been detected. In contrast to lakes and oceans, estuaries and coastal shelf waters tend to be N limited, with some exceptions. Water quality managers may question the reason for this, as the three case studies described earlier, especially temperate estuaries and the coastal shelf, appear to be N limited and not P limited. Such an understanding is basic to arguments about cause and effect and also what ecosystem conditions drive a coastal ecosystem toward N limitation or P limitation. Smith provided an explanation that still has merit.

Smith posited that the apparent difference in limiting nutrient between lakes and oceans lies, in part, with the relative rates for material exchange via physical processes of advection (i.e., transport of water and associated constituents) and eddy diffusion (i.e., local transport of material against a concentration gradient) and biogeochemical processes of N fixation and fixed N loss. The argument is based on field experiments in marine embayments with little or no freshwater input, so advective transport of nutrients from the land simplified nutrient budget development. Smith postulates that if the physical exchange rates are long (e.g., open ocean), then the system would tend toward P limitation because biogeochemical adjustment of the N:P availability ratio is short compared with long physical exchange rates (e.g., months to a year or longer). In other words, nitrogen fixation would balance any losses of nitrogen associated with phytoplankton sedimentation, but P has no atmospheric reservoir or biochemical mechanism for an equivalent P fixation to occur. If the physical exchange rates are faster than biochemical rates (e.g., nitrogen fixation), then net ecosystem production (and by inference net phytoplankton biomass production) of organic material may be N limited; if the biochemical rates are faster, then net production will tend toward P limitation. The ratio of the residence time of the water to the biogeochemical turnover rate indicates the degree to which the hydrodynamic processes dominate or modify estuarine ecosystems (Day et al. 1989). This is an example of the importance of scaling critical processes (Harris 1986). Smith’s conceptual model should apply to estuaries and shelf waters. Smith’s data, analysis, and synthesis and other empirical data support N limitation in estuaries and coastal shelf environments.

The concept of scale is another element of the conceptual framework. Physical processes that modify the expression of bloom dynamics will best be detected at the ecological level (Figures A-1, A-2). In this context, Geyer et al. (2000) cite many examples supporting the observation that “at virtually every spatial scale, within every component of estuarine ecosystems, physical processes influence the distribution and fate of chemicals (*sic* including nutrients) and organisms.” Physical processes are involved in the delivery of nutrients to the biota in estuaries and coastal shelf waters, and also fundamentally influence advective and dispersive processes that transport and retain dissolved and particulate material, including nutrients and plankton in estuaries and on the coastal shelves. The roles of physical processes influencing net biomass production of phytoplankton are explored in the main text in more detail.

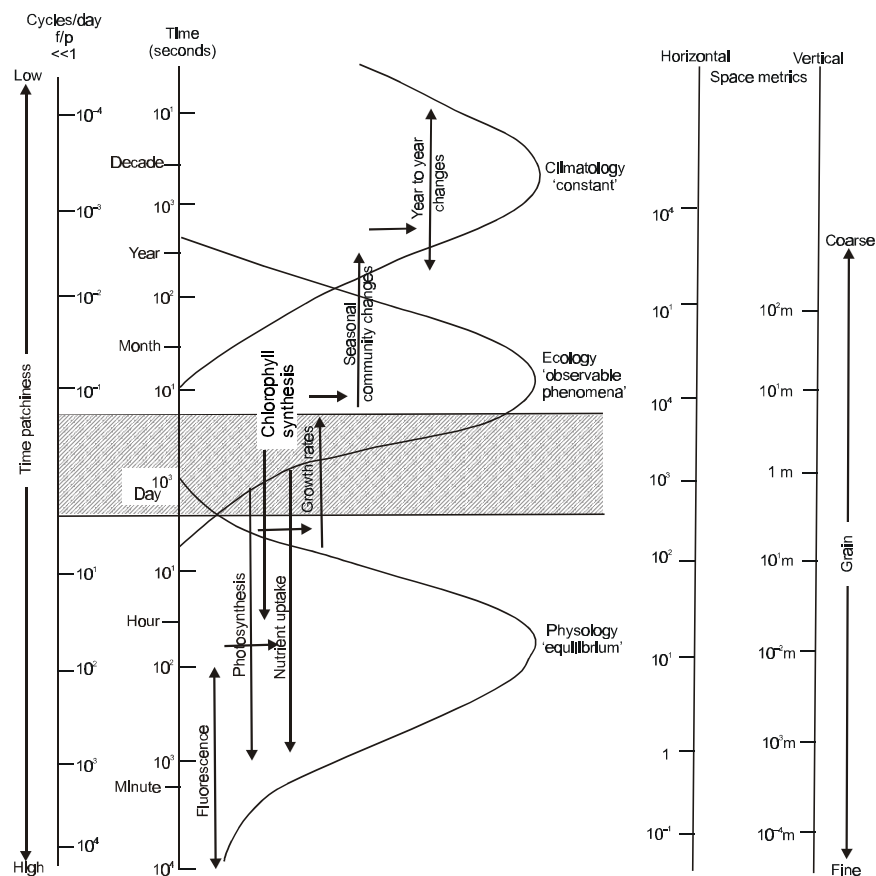


Figure A-1. Scales of phytoplankton ecology. Horizontal and vertical scales are determined by the respective diffusion coefficients K_h and K_L . The time scales for the algae are determined by the scales of growth (shaded band). The processes of importance at each scale are noted. In the past it was always assumed (wrongly) that physiological processes were at equilibrium and that climatological variability could be ignored. Source: Harris 1986.

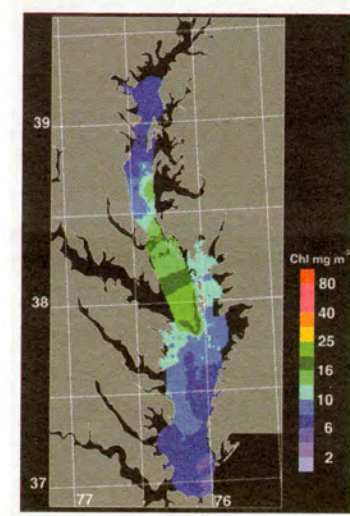
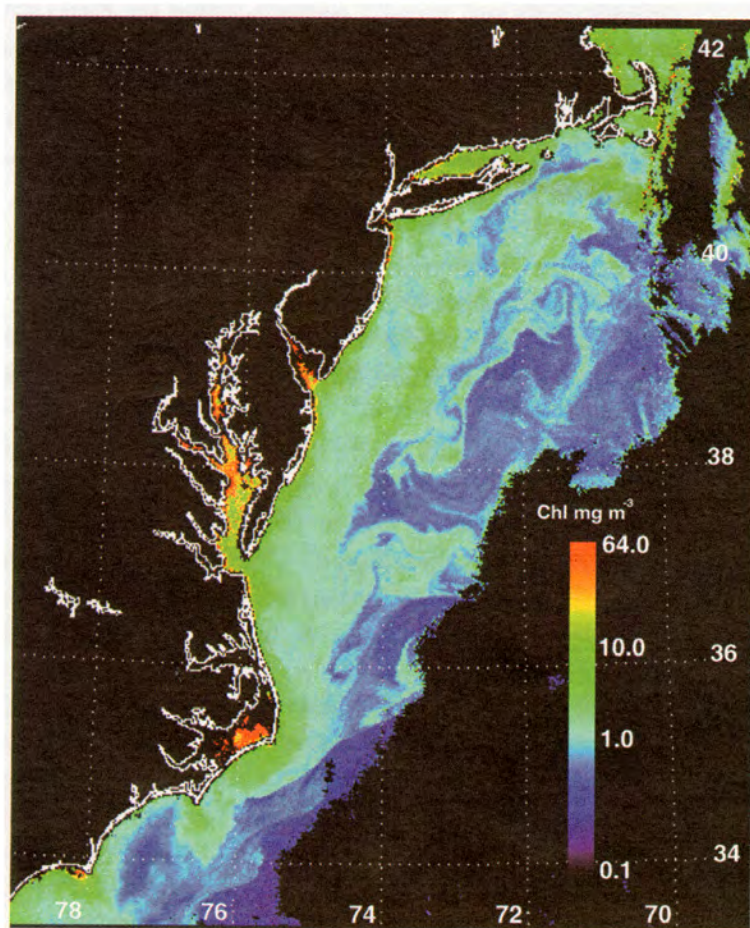


Figure A-2. The left panel shows the distribution of chlorophyll—an indicator of algal biomass—along the east coast of the U.S. from Boston to South Carolina as measured from the ocean color satellite SeaWiFS. Note the higher chlorophyll levels closer to shore, and the much higher levels in enclosed bays, such as Pamlico Sound (latitude 35°) and Chesapeake Bay (mouth at 37° latitude). The above panel shows chlorophyll distributions within Chesapeake Bay in more detail, as measured during a phytoplankton bloom. Both images were taken in April 1998. Source: Howarth et al. 2000.

APPENDIX B

ADDITIONAL INFORMATION ON THE ROLE OF TEMPERATURE AND LIGHT ON ESTUARINE AND COASTAL MARINE PHYTOPLANKTON

Availability in temperature and light values can be plotted as hydroclimographs (e.g., polygons) to picture their relative seasonal change around the coasts. A temperature increase will lower the density of seawater and contribute to density stratification. In particular, rapid changes in water temperature influence the rate of biological metabolic processes, including algal growth rates (Eppley 1972). Some species exhibit various degrees of thermal adaptation when temperature changes are gradual.

Speculation suggests that if sea temperatures continue to rise as a function of the “greenhouse effect,” estuarine biotic communities may change over the next several decades as they approach thermal limits. For example, although the seagrasses *Halodule* (shoalgrass) and *Zostera* (eelgrass) now overlap in Core Sound, NC, a northward migration of *Halodule* and a retreat of *Zostera* may occur if water temperatures rise faster than populations can adapt. Such relationships and their potential alteration probably can be documented for other biotic groups along other coasts. For example, if temperature now limits regular flowering of the seagrass *Thalassia* (turtle grass) along the northern Gulf of Mexico, then increased flowering may occur if temperatures warm. Such conjectures notwithstanding, however, little information is available to help assess the consequences of a potential interaction between an increased temperature rise and increased nutrient supply on seagrasses.

Light has a fundamental role in aquatic primary production and is essential in the development of models to estimate phytoplankton primary production (Behrenfeld and Falkowski 1997) and submerged aquatic vegetation (Dennison et al. 1993). Many concepts in aquatic ecology are based on the light gradient (Huisman 1999) (e.g., diel plankton vertical migration, benthic animals migrating out of sediments, depth of euphotic zone, and mixing depth). Phytoplankton growth, nutrient relationships, light, and other physical processes interact in a feedback system. Although light may be adequate and all other requirements met for their formation, blooms may not form if dispersive processes are greater than algal cell doubling time (Kierstead and Slobodkin 1953; Lucas et al. 1999). Tidal ranges greater than approximately 2.0 m apparently disperse phytoplankton faster than cell doubling time, even if nutrient conditions would be supportive of a bloom (Monbet 1992).

Both the vertical distribution of phytoplankton abundance and community composition are frequently changing in the water column. Swimming through use of a flagellum, especially by dinoflagellates, and changes in cell density through physiological mechanisms allow modest vertical mobility against weak mixing forces. If the mixing depth is substantially greater than the euphotic zone depth (e.g., a depth where approximately 1% of surface insolation occurs), then phytoplankton spend too much time in an inadequate light environment and net primary production is limited (Figure B-1) (Huisman et al. 1999). The compensation depth is where water column phytoplankton photosynthesis and respiration are in balance, and this often approximates the 1% insolation depth, or about two times the Secchi disc depth (Parsons and Takahashi 1973). For example, in the lower Delaware Bay the upper-mixed layer often corresponds to the bay bottom, the result of which is that phytoplankton spend too much time below the compensation depth and hence low biomass production occurs (Pennock 1985). In systems where the dominant support of the food web is derived from photosynthesis, net phytoplankton production must be large enough to support the microbial loop (Azam et al. 1983) and higher trophic levels.

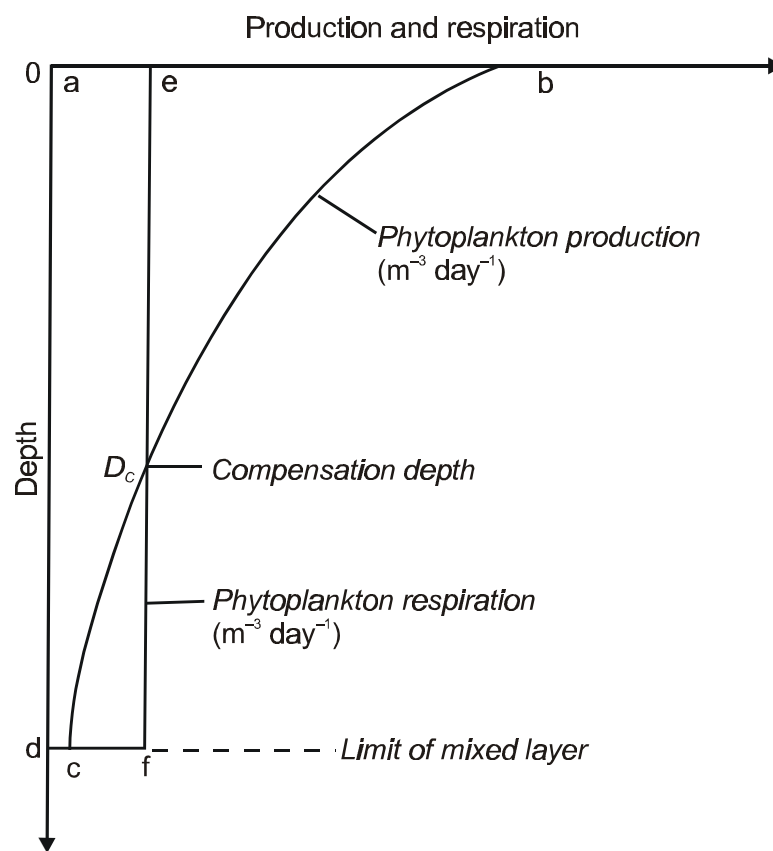


Figure B-1. Diagram illustrating theoretical distribution of phytoplankton production and phytoplankton respiration. After Sverdrup (1953). Source: Mann and Lazier (1996).

In a homogeneous medium, light decreases exponentially with depth and can be represented by the negative exponential equation:

$$I_z = I_0 e^{-kz}$$

where I_z is light quantity at depth z , I_0 is the light quantity at the water surface, and k represents the vertical light extinction coefficient; the extinction coefficient is more easily calculated as the base \log_{10} : $0.434 kz = \log I_0 - \log I_z$. The light gradient also often extends longitudinally down estuaries, especially those dominated by large volumes of sediment-bearing freshwater. In highly turbid estuaries, deepest light penetration shifts toward the orange end of the spectrum (Champ et al. 1980). The euphotic zone depth generally increases from the tidal head to the coast. Where turbidity is at its maximum level, a localized sharp decrease in euphotic zone depth is typical (Flemer 1970; Pennock and Sharp 1986). Regions with the greatest turbidity typically are light-limited or almost so. In the turbid upper Chesapeake Bay, riverine loading supplied nearly 90% of the particulate organic carbon, but in the clearer waters of the mid-bay primary production dominated supply at 97% (Biggs and Flemer 1972); Smith and Kemp (1995) have updated their original estimate and suggest a lower percentage. However, much of the allochthonous organic matter may not be biologically available. In waters of high humic material content (e.g., Charlotte Harbor, FL), light attenuation can be severe (Dixon and Kirkpatrick 1999). The interaction between turbidity caused by humic materials and nonchlorophyll-bearing

particulates complicates the direct application of the Secchi disc as a measure of nutrient overenrichment. Spectral radiometers can to some extent partition the various components of light extinction and are the preferred tools. Modern algal pigment diagnostic tools (e.g., HPLC) can compare water quality responses to varying nutrient and other pollutant inputs across various coastal system types (Jeffery et al. 1997). It is possible that turbidity may mask the impending development of undesirable algae.

The vertical extinction coefficient for estuaries shows wide seasonal variations. Values frequently exceed 0.1 m^{-1} . The extinction in open-ocean waters is often estimated by the relation $E.C. = 1.7/\text{Secchi depth in meters}$. Holmes (1970) and Keefe et al. (1976) both arrived independently at a constant of approximately 1.46 instead of 1.7 for turbid estuarine and nearshore coastal waters. Walker (1980) suggested that the original Poole and Adkins (1929) Secchi disc constant on average gives results approximately 17% too high and suggested a value of 1.45. These corrections should be made and, more importantly, it is useful for the constant to be checked for each estuary. For more quantitative work, a quantum light meter that measures over a spectral range of 400-700 nm is preferred. Commercial products (e.g., www.licor.com) are now available that can measure the spectral photon flux over a range of interest to aquatic scientists.

The extinction coefficient can be broken down into several components. The total light attenuation, $K_T = K_w + K_c + K_d + K_p$ (Lorenzen 1972; Kirk 1983; Bledsoe and Philips 2000; Koenings and Edmondson 1991) can be resolved for the effects of water, chlorophyll *a*, dissolved substances, and nonalgal particulate matter. In many estuaries, K_d may contribute between 5% and 50% of the K_T . The K_w usually can be ignored because it is such a minor component. In blackwater estuaries receiving high loads of humic materials the K_d may dominate K_T . In systems such as the “turbidity maximum zone” in upper Chesapeake Bay, K_p may be the dominant component. The EPA Chesapeake Bay Program has sponsored research to calibrate K_T components applicable to SAV beds (www.chesapeakebay.net; search the publications database for “Chesapeake Bay Submerged Aquatic Water Quality and Habitat-Based Requirements and Restorations Goals: A Second Technical Synthesis.”

Among some coastal ecosystems, light (i.e., mean photic depth) and nutrient loading appear to be equally good predictors of phytoplankton primary production (see Figure 1b in Cloern 1999). This observation strengthens the proposition that phytoplankton production in these systems can be limited by other resources and processes in addition to nutrient loading. Pennock and Sharp (1994) suggest that the Delaware River Estuary functions analogously as a chemostat during the summer. They point out that high N supplies from upstream advect continually through the brackish-water region into the lower estuary, where high primary production occurs from remineralized N and the advected supply and the phytoplankton biomass is limited by grazing. Their conclusion is especially significant because evidence also suggests that bioassay experiments that isolate the water may lead to misidentification of nutrient limitation. The flushing component in the bay provides the physical analogue to a chemostat, where the nutrient supply and adequate light support high phytoplankton biomass production and grazing and flushing maintain a potentially steady-state phytoplankton biomass, with fluctuations due primarily to physical forcing factors.